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**Solar radiation and functional traits explain the decline of forest primary productivity along a tropical elevation gradient**

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# Solar radiation and functional traits explain the decline of forest primary productivity along a tropical elevation gradient

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**Data accessibility statement:** We confirm that, should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository and the data DOI will be included at the end of the article.

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## Abstract

A mechanistic understanding of environmental controls on ecosystem productivity remains surprisingly elusive and controversial. Tropical forest environmental gradients present a particularly rich study system for facilitating insights into the relationships between environment, biodiversity and ecosystem function. In this study, we integrated a generic framework for scaling plant growth, carbon fluxes, and functional trait spectra within an individual-based forest model, to analyse variation in forest primary productivity along a 3.3 km tropical elevation gradient in the Amazon-Andes. The model accurately predicted the magnitude and trends in forest productivity with elevation, with solar radiation and plant functional traits collectively accounting for productivity variation along the gradient. Solar radiation influenced the magnitude of forest productivity with upland sites being less productive, while the variation of plant functional traits (leaf dry mass per area, leaf nitrogen and phosphorus concentration and wood density) with elevation regulated the sensitivity of productivity to changes in elevation. Remarkably, explicit representation of temperature variation with elevation was not required to achieve accurate predictions of forest productivity. The turnover in the plant community and ensuing shift in leaf traits, a possible indirect response to temperature, cancels much of the temperature dependency that is found in single plant measurements of photosynthesis. Light competition is an important process that should be explicitly accounted for in order to accurately simulate forest productivity. Our semi-mechanistic model shows that spatial variation in traits can translate into potentially mapping spatial variation in productivity at the landscape scale.

1. Introduction

One of the major challenges in contemporary ecosystem science is to understand how ecosystems respond to changes in environmental conditions, and how taxonomic and functional diversity mediate these changes (Lavorel & Garnier 2002; Balvanera et al. 2006). Environmental conditions change both in time and in space, and transects along environmental gradients can provide valuable insights into controls of ecosystem function. Tropical forest environmental gradients present a particularly rich study system (Vazquez & Givnish 1998; Wright 2002), with their high diversity facilitating general insights into the relationships between diversity and function that are not contingent on the characteristics and presence or absence of particular dominant species. More specifically, tropical elevation gradients, with their usual high levels of moisture and year-long growing season, provide “natural laboratories” in which to understand the influence of temperature on ecosystem function without the complicating influence of variation in temperature seasonality and winter dormant seasons (Malhi et al. 2010; Sundqvist et al. 2013).

It is valuable to distinguish direct environmental controls on ecosystem productivity from indirect controls mediated through forest structure and composition, as direct and indirect controls can have different response times to environmental change, and determine the degree to which productivity can be estimated from surveying ecosystem composition. Environmental conditions are usually considered direct drivers of ecosystem productivity (Fig 1). Although in most tropical regions temperature is not a limiting factor on productivity, some studies suggest that across sites, tree growth increases with mean temperature (Raich et al. 2006, Cleveland et al. 2011) within the temperature range of currently observed tropical climates. In seasonal tropical forests, rainfall is positively associated with tree growth (Brienen & Zuidema 2005), while other studies identify solar radiation as a key driver of forest productivity across Amazonia (Nemani et al. 2003) particularly during the rainy season (Graham et al. 2003). Soil fertility may be important: in lowland tropical forest, phosphorus (P) availability is considered a key limiting factor of primary productivity (Quesada et al. 2012) whereas in montane regions with colder and younger soils, nitrogen (N) may be the limiting factor (Tanner et al. 1998). In summary, increases in one of the above factors can have positive effect on tree growth (given no other resource limitation), expressing a direct (“proximal”) and short-term effect of environmental conditions on ecosystem productivity (Fig 1).

Environmental conditions can additionally have an indirect (“distal”) effect on forest productivity by regulating the structure and/or the species/functional composition of the community (Fig 1). Such effects tend to act on longer temporal scales, where potential feedbacks between structure and functional composition can also take place. Many studies have shown that functional traits systematically vary with water availability (Santiago et al. 2004), soil fertility (Fyllas et al.



2009) and stand development (Lebrija-Trejos et al. 2010) and trait variation can predict individual-tree growth rate (Poorter et al. 2008) and community productivity (Finegan et al. 2014). However feedbacks between environmental conditions, stand structure and functional composition have also been identified. For example, across Amazonia there exists a structural feedback on productivity, with rich soils favoring low biomass, fast-growing species in contrast to poor soils that favor high biomass slow-growing species (Baraloto et al. 2011; Quesada et al. 2012).

Disentangling the role of environmental and biotic controls on tropical forest productivity requires appropriate datasets. In recent years, a large body of data has been emerging from an elevation transect in the Andes and Amazon in SE Peru, including rates of ecosystem carbon cycling (Girardin et al. 2010; Malhi et al. 2017a; Nottingham et al. 2015), forest structure and dynamics (Feeley et al. 2011; Asner et al. 2014a), plant ecophysiology (van de Weg et al. 2009; 2012; Bahar et al. 2016) and leaf and wood traits (Asner et al. 2014b; Malhi et al. 2017b). Along this 3300 m gradient there is a steep temperature decrease with increasing elevation, a reduction in solar radiation, and an increase in soil N and P content that drive high species turnover (Neyret et al. 2016). This species turnover is associated with shifts in several functional traits including increasing leaf mass per area (*LMA*) and leaf P concentration with elevation (Asner et al. 2014b). Forest stature and structure vary greatly between lowland and highland plots, resulting in a decline in biomass with elevation and more open forests in the mountains (Malhi et al. 2017a; Asner et al. 2014a). Productivity declines with elevation but with some evidence of a step-change decline near the cloud base (Malhi et al. 2017a). It thus seems that various direct and indirect factors can potentially control forest productivity along the Andes-Amazon gradient. The integration of the available datasets presents a unique opportunity to mechanistically explore the influence of climate, plant functional traits and forest structure on forest productivity.

Individual-based vegetation models provide an ideal framework to integrate forest inventory data with ecosystem dynamics theory and to explore how climate, functional traits and stand structure control primary productivity (Purves & Pacala 2008). In particular, by accounting for inter-specific functional variation as well as tree-size variation, the performance of alternative life history strategies can be explored (Moorcroft et al. 2001; Scheiter et al. 2009). Mechanistic, process-based vegetation models apply detailed energy, carbon and water flux algorithms to quantify how key ecosystem processes vary with environmental conditions and tree functional traits, the latter extensively used as predictors of plant processes (Scheiter et al. 2013). For example, *LMA* and mass-based leaf nitrogen ( $N_{Lm}$ ) and phosphorus ( $P_{Lm}$ ) concentration are the central elements of the leaf economic spectrum and can be used to predict mass-based photosynthetic and respiration rates (Wright et al. 2004; Atkin et al. 2015), while wood density ( $\rho_w$ ) and maximum height ( $H_{max}$ ) appear



to be good predictors of tree growth and mortality rates (Poorter et al. 2008; Wright et al. 2010). Process-based vegetation models usually implement detailed photosynthetic algorithms (Farquhar et al. 1980) to calculate rates of CO<sub>2</sub> assimilation and then allocate C to different plant components (Franklin et al. 2012). However, such models can be challenging to parameterise and computationally expensive to run at individual-tree scale. As an alternative approach, Enquist et al. (2007) suggested a framework that employs a growth equation which integrates functional traits with tree-size and can be used to estimate individual growth rates for each tree in a stand in a much simpler way. In our current study we make changes to an existing vegetation model (TFS, Fyllas et al. 2014) that replace the detailed physiological algorithms with a general trait-based growth equation.

The aim of our paper is to apply the TFS model to disentangle the relative importance of climate (direct environmental effects), stand structure and functional traits (indirect environmental effects) in controlling forest productivity along the Andes-Amazon elevation gradient. We initially apply TFS along the gradient and validate its performance against field-based estimates of productivity. We subsequently exploit the model framework to perform a set of randomisation exercises designed to quantify the relative importance of climate, stand structure and functional traits in determining the observed patterns of forest productivity.

**2. Materials and Methods**

**2.1 Study site**

The study area is located along a 3300 m elevation gradient in the tropical Andes and extends to the Amazon Basin. Across this transect a group of nine intensively monitored 1-ha plots (Table S1.1) was established as part of the long-term research effort coordinated by the Andes Biodiversity Ecosystems Research Group (ABERG, <http://www.andesconservation.org>) and the ForestPlots (<https://www.forestplots.net/>) and Global Ecosystems Monitoring Network (GEM; <http://gem.tropicalforests.ox.ac.uk/projects/aberg>) networks. Five of the plots are montane plots in the Kosñipata Valley, spanning an elevation range 1500 - 3500 m (Malhi et al. 2010), two are submontane plots located in the Pantiacolla front range of the Andes (600 - 900 m) and two plots are found in the Amazon lowlands in Tambopata National Park (200 - 225 m). The elevation gradient is very moist (Table S1.1), with seasonal cloud immersion common above 1500 m elevation (Halladay et al. 2012), and no clear evidence of seasonal or other soil moisture constraints throughout the transect (Zimmermann et al. 2010). Plots were established between 2003 and 2013 in areas that have relatively homogeneous soil substrates and stand structure, as well as minimal evidence of human disturbance (Girardin et al. 2014).

At all plots, the GEM protocol for carbon cycle measurements has been applied. For six of the plots, the net primary productivity (NPP, the rate of biomass production in wood, canopy and fine roots) and gross primary productivity (GPP, the rate of canopy carbon uptake through photosynthesis) were estimated by summation of the measured and estimated components of NPP (litterfall, woody production, fine root turnover and branch turnover) and autotrophic (leaf, wood and fine root) respiration (Malhi et al. 2017a). For the remaining plots, we used measured NPP to estimate GPP applying the mean carbon use efficiency ( $c = \text{NPP}/\text{GPP}$ ) of the other plots, separated into cloud forest and submontane/lowland plots. Further details of measurement protocols are given in Malhi et al. (2017a) and summarised in S1.

## 2.2 Model Description

The original TFS model is a trait-continua and individual-based model, which simulates the carbon (C) balance of each tree in a stand (Fyllas et al. 2014). Rather than grouping trees into plant functional types, TFS prescribes inter-related joint distributions of functional traits which represent trade-offs of possible plant strategies and responses to environmental conditions. The model is initialised with tree-by-tree diameter at breast height ( $D$ ) and functional traits data. Three leaf traits ( $LMA$ ,  $N_{Lm}$ ,  $P_{Lm}$ ), the central components of the leaf economic spectrum, regulate the photosynthetic capacity and the respiration rate of trees. Wood density ( $\rho_w$ ) accounts for variation in aboveground biomass ( $M_A$ ), with trees of greater  $\rho_w$  supporting higher biomass. Allometric equations are used to infer tree height ( $H$ ) and allocation to leaf ( $M_L$ ), stem ( $M_S$ ) and root ( $M_R$ ) biomass. Light competition is approximated using the perfect plasticity assumption (Strigul et al. 2008). The carbon and water balance of each tree is estimated on a daily time-step and at the end of each year stand-level GPP and NPP is estimated by summing up the daily individual-tree C fluxes.

Here we use a simplified version of TFS (described in S2), where the mechanistic representation of photosynthesis, respiration and C allocation is replaced with the integrative whole-plant growth rate model of Enquist et al. (2007):

$$\frac{dM_T}{dt} = \left(\frac{c}{\omega} A_L\right) \left(\frac{a_L}{m_L}\right) M_L \quad (1)$$

where  $M_T$  is the total plant dry biomass (kg),  $c$  the carbon use efficiency (no units),  $\omega$  the fraction of whole-plant dry mass that is carbon,  $A_L$  the leaf area specific photosynthetic rate ( $\text{g C cm}^{-2}$  per unit time),  $a_L$  the individual leaf area ( $\text{cm}^2$ ),  $m_L$  the individual leaf mass (g) and  $M_L$  the total leaf dry mass (kg).

Equation (1) is an extension of the classic relative growth rate equation (Hunt 1982), with the basic assumption that whole-plant net biomass growth rate scales isometrically with total plant leaf

biomass. Predicting the patterns of plant biomass allocation is a topic of extensive debate with Metabolic Scaling Theory (MST) suggesting relative invariant power laws and other studies arguing that scaling varies across species and plant sizes (Poorter et al. 2015). Another critique of MST-based growth equations is that they do not take into account resource availability and in particular the vertical distribution of light in forest stands (Muller-Landau et al. 2006; Coomes & Allen 2009). In order to implement equation 1 within TFS and deal with these critiques we 1) used a set of allometric equations with stochastic scaling coefficients estimated from available data and 2) expressed the photosynthetic rate  $A_L$  as a function of both leaf traits (that vary in a continuous way within and between communities) and irradiance that takes into account competition for light between individuals. In the following paragraphs we describe how the model was constrained with the available field and literature data. A sensitivity analysis of the simulated GPP and NPP for some of the key model parameters is provided in S2.

### 2.2.1 Tree allometry

Transect-wide allometric equations of tree height ( $H$ ) and crown area ( $C_A$ ) as a function of tree diameter were used to define the architecture of each tree in a stand (Shenkin et al. in review). In the model, trees were considered to have a flat-topped circular canopy with an area equal to the allometrically estimated projected crown area.

In TFS aboveground tree biomass ( $M_A$  in kg) is estimated from the Chave et al. (2014) equation that takes into account the diameter, the wood density and the height of a tree. Total leaf biomass was expressed as a power function of  $M_A$ , parameterised using the BAAD dataset (Falster et al. 2015). During simulations we allowed the coefficients of the power functions to vary within their 95% confidence interval estimates, with individual trees having different leaf allometries (S2–Tree Allometry).

### 2.2.2 Functional traits and Photosynthesis

The photosynthetic rate ( $A_L$ ) is controlled by the leaf functional traits and the available light of each individual. A Michaelis-Menten (MM) model was used for that purpose where:

$$A_L = \frac{A_{\max} I}{k + I} - R_d \quad (2)$$

with  $I$  ( $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) the irradiance at the top of each individual,  $A_{\max}$  the maximum gross photosynthetic rate ( $\mu\text{mol m}^{-2}\text{s}^{-1}$ ),  $k$  the half saturation coefficient ( $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) and  $R_d$  is the non-photorespiratory mitochondrial  $\text{CO}_2$  release taking place in the light (i.e. respiration in the light) ( $\mu\text{mol m}^{-2}\text{s}^{-1}$ ).

The irradiance  $I$  is estimated through the light competition scheme, while the three leaf functional traits ( $LMA$ ,  $N_L$  and  $P_L$ ) regulate the parameters of the light response curve (Marino et al. 2010). An independent dataset of 136 light response curves and  $LMA$ ,  $N_L$  and  $P_L$  measurements (Atkin et al. 2015; Weerasinghe 2015) was available for 14 study sites along the Andean elevation gradient. These data were used to fit MM light response curves and express their parameters ( $A_{max}$ ,  $k$  and  $R_d$ ) as a function of the leaf functional traits (S2-Photosynthesis). An average daily  $A_L$  is estimated using equation 2 and average daily irradiance, with the total daily  $A_L$  given after multiplying average  $A_L$  with the day length.

Analyses in Bahar et al. (2016) and here (S2-Photosynthesis) suggest that across the Andean gradient the maximum light-saturated photosynthetic rate does not vary with elevation. Thus photosynthesis strongly acclimates to prevailing air temperature and this supports the use of a temperature independent model of leaf photosynthesis in our simulations. However, in order to specifically test for the importance of direct temperature effects on photosynthesis, we used a generic temperature sensitivity model (Higgins et al. 2016) and compared simulations with and without temperature dependence. In this wet gradient (Zimmermann et al. 2010) we did not include any water availability effect on photosynthesis.

### 2.3 Model - Inventory data integration

Within our study plots all trees with a  $D > 10$  cm have been identified at the species level, and in selected subplots all trees with  $D > 2$  cm have been measured and identified. In addition  $LMA$ ,  $N_{Lm}$ ,  $P_{Lm}$  and  $\rho_w$  were available (Malhi et al. 2017b; Asner et al. 2016b) for approximately 7% of the stems of species that comprise 60% (in diverse lowland sites) to 80% (in the less diverse montane sites) of the total plot basal area. In our simulations individuals with measured trait values were included as such, without using an average species value, in order to incorporate intraspecific variation. For the rest of the trees, trait values were populated hierarchically using, in decreasing order of preference, the species mean plot value, the species transect-wide mean value or, for trees for which no species-level traits were available, the plot-level trait means.

Climate data were available from weather stations located close to each study site (Table S1.1). The most complete time series for most weather stations were for the year 2013 and solar radiation, temperature and precipitation were recorded at 30-minute intervals. We used these time-series to estimate average daily climate. For days with missing data, the average daily values were estimated by interpolating the daily parameters of the previous and following three days.

2.4 Simulations

We performed two sets of simulations to elucidate the major controls of forest productivity along Amazon-Andes gradient. Firstly, the importance of temperature sensitivity was explored following a “leave-one-out” procedure that explored the ability of TFS to simulate GPP and NPP patterns under three different model setups: 1) inclusion of both photosynthetic temperature sensitivity and variation of functional traits along the gradient, 2) inclusion only of photosynthetic temperature sensitivity, and, 3) inclusion only of functional trait variation.

Secondly to explore the importance of climate, stand structure and functional traits in determining GPP and NPP across our study sites, we applied within TFS a set of randomization exercises. These are described in detail in S3. To test the importance of climate (*Climate only Setup* - *CoS*), we simulated GPP and NPP by using the local (plot-specific) climate and a regional average stand structure and trait distribution (*i.e.* the average stand structure and traits distribution across all plots along the transect). The hypothesis behind *CoS* is that climate, and particularly variation in incoming solar radiation, is sufficient to explain variation in productivity across the elevation gradient, with no between-plots variation in traits or stand structure required. The role of stand structure was tested using the *Structure only Setup* (*SoS*). Following this setup, the observed *D* distribution in each plot was used to initialise trees, while climate and functional diversity were kept constant. The hypothesis behind the *SoS* is that change in stand structure, via its effects on the partitioning of available light, is the most important determinant of productivity along the elevation gradient. Finally, the potential control of functional trait variation, expressed through the distributions of the four traits, was explored by initializing TFS with the locally observed trait distribution while keeping climate and stand-size distribution fixed (*Traits only Setup* (*ToS*)). The hypothesis tested by this setup is that knowledge of the local distribution of the four functional traits is adequate to predict observed variation in GPP and NPP with elevation.

3. Results

The predictive ability of the various model setups were quantified through standardised major axis (SMA) regressions and estimation of root mean square error (RMSE in  $\text{MgC ha}^{-1} \text{y}^{-1}$ ) between observed and simulated GPP and NPP. In addition ordinary least square regressions of simulated GPP and NPP with elevation were performed with the estimated slope ( $\beta_{\text{OLS}}$  in  $\text{MgC ha}^{-1} \text{y}^{-1} \text{km}^{-1}$ ) representing the sensitivity of each setup to changes in elevation.

Simulations including photosynthetic temperature sensitivity and functional trait shifts along the gradient over-predict sensitivity to elevation changes, underestimating both GPP and NPP

particularly at upland sites [GPP: RMSE=9.75,  $\beta_{OLS}$ =-8.90, NPP: RMSE=2.86,  $\beta_{OLS}$ =-2.94] (Fig 2, Table S5.1). A similar model behavior was observed even when only temperature sensitivity was included, assuming no functional traits shift with elevation. However, when trait values were allowed to vary with elevation in accordance with observations and temperature sensitivity was excluded, the model performed best [GPP: RMSE=3.25,  $\beta_{OLS}$ =-4.24, NPP: RMSE=0.99,  $\beta_{OLS}$ =-1.40]. We named this model setup, initialized with plot specific solar radiation, stand structure and functional traits data, as the fully constrained model setup (*FcS*). We note here that accounting for light competition was particularly important for accurate GPP and NPP simulations (Fig S5.2, Table S5.2). The *FcS* captures the broad gradient between higher productivity in lowland sites and lower productivity in montane sites, suggesting that direct photosynthetic temperature sensitivity could be excluded from our modelling framework (although it could still matter through its effects on traits), and that across the gradient solar radiation is the main climatic driver of spatial variation in forest productivity.

After validating the model, we used the randomization exercises to test the importance of climate, stand structure and functional traits to drive GPP and NPP patterns. When exploring for the effects of climate (*CoS*), *i.e.* factoring out stand structure and traits variation, the RMSE increased both for GPP and NPP [3.99 and 1.99 respectively] and the model was less sensitive to elevation changes [ $\beta_{OLS}$ =-1.40 and  $\beta_{OLS}$ =-0.46 respectively] (Table 1). Hence, *CoS* captured the mean productivity across the gradient but was not as sensitive as *FcS* to changes in elevation and in particular overestimated forest productivity at upland sites (Fig 3).

When site-specific structure was used as the main driver (*SoS*), there was a substantial decline in the predictive ability of the model. The broad scale decline of primary productivity with elevation could not be reproduced adequately (Fig 3), and RMSE increased both for GPP and NPP (Table 1). This suggests that knowledge of the tree-size distribution alone is not enough to estimate patterns of productivity along the Andean elevation gradient. It should be remembered however that the *SoS* setup represents mainly variation in size-class distribution and not variation in established biomass, which in the model is additionally influenced by variation in wood density.

When functional trait variation alone was considered (*ToS*), the model reproduced the broad scale decline with elevation but both GPP and NPP were overestimated compared to *FcS*, particularly at mid elevations (Fig 3). For GPP the RMSE increased [5.38] compared to the *FcS* and the *CoS* but the sensitivity of the model to elevation was close to observations [ $\beta_{OLS}$ =-3.26] (Table 1). For NPP, the RMSE [1.64] was higher than *FcS* but lower than *CoS* and sensitivity with elevation [ $\beta_{OLS}$ =-1.08] was higher than *CoS*. These results suggest that the local traits distributions



captures the declining trend in productivity with elevation, but additional knowledge of solar radiation, is required to accurately estimate GPP and NPP.

To gain further insights into the mechanisms that drive variation in forest productivity, we explored how some key stand-level parameters vary with elevation using inferences from the *FcS* (Fig 4). Average light availability over all canopy depths ( $I$ ) declines with elevation and then increases at the uppermost plot, following variation in incoming solar radiation at the top of the canopy ( $S_0$ ) and inversely the number of stems per area ( $N_S$ ). On the other hand, the basal-area weighted average  $LMA$  and  $P_{La}$  increase with elevation, while  $N_{La}$  does not change much. Simulated  $R_d$  does not vary much across the gradient and given the constant  $A_{max}$  the decline in actual photosynthesis ( $A_L$ ) is mainly a result of variation in light availability, with a small divergence at the uppermost plots. However, the half-saturation coefficient also increases with elevation and this suggests that trees at upland sites have a lower photosynthetic rate for a given light intensity (below maximum rates) compared to their lowland counterparts, explaining the divergence in  $A_L$ . Thus reductions in average photosynthetic rate with elevation are likely to be mainly due to reductions in light availability as well as due to the higher light levels required for photosynthetic light saturation for trees at higher elevations.

#### 4. Discussion

Various environmental and biotic drivers can control forest productivity along the Amazon-Andes elevation gradient (Fig 1). We developed a simplified version of a vegetation model that integrates a range of field measurements in order to understand the relative importance of climate, stand structure and functional traits on forest productivity. The inclusion of the trait-based growth equation of Enquist et al. (2007) increases the simplicity and tractability of the model. Overall, TFS provided simulations that were in line with observations of the magnitude and trends in GPP and NPP across the elevation gradient. In the following paragraphs we describe how the performed simulations and randomisation exercises were used to understand the decline in productivity with elevation.

##### Temperature and Photosynthesis Acclimation

Variation in primary productivity has been traditionally considered to reflect the effects of climate variables such as radiation, temperature and precipitation on plant metabolic rates (Chapin et al. 2012). A recent study reported that, along the Andean elevation gradient, maximum carboxylation and electron transport rates at a standardized temperature of 25°C were significantly higher at upland sites, possibly reflecting greater  $P$  per unit leaf area at high elevations and/or thermal



acclimation to sustained lower growth temperatures (Bahar et al. 2016). By contrast, when measurements of gas exchange were made at the daytime temperatures at each site (20–28°C; Fig S2.2), light-saturated, area-based rates of net photosynthesis, as well as maximum carboxylation and electron transport rates, show no significant trend with elevation (Bahar et al. 2016, Malhi et al. 2017a). The latter observations support the use of a temperature-independent equation for photosynthetic carbon assimilation. Our simulations show that accurate GPP and NPP predictions can be made without a direct temperature sensitivity effect on photosynthesis (Fig 2). When both temperature sensitivity and functional traits variation was included in the model, forest productivity was too sensitive to elevation changes. This suggests that the effect of temperature is likely to be manifested through variation in leaf traits, which may be controlled by variation in environmental conditions (including temperature) along the gradient. The shift in leaf traits and photosynthetic characteristics with elevation cancels out much of the ecophysiological temperature dependency found in single plant measurements. This does not imply that short-term temperature changes (months to decades) will not affect forest productivity but rather that long-term changes lead to a turnover in species such that the local community is acclimated to local growing conditions, resulting in little sensitivity of productivity to temperature on long time scales, and within the temperature range studied. An alternative possibility is that temperature shows a strong but non-causal relationship with leaf traits along the gradient, and this obscures a real direct temperature effect.

### Functional Traits

Previous studies along this and other elevation gradients in the Andes region found that more than 80% of  $LMA$  and  $N_L$  turnover between communities is determined phylogenetically, suggesting that these traits may have been involved in evolutionary adaptation (Asner et al. 2014b). Furthermore, Asner et al. (2014b) found that these inter-community differences in  $LMA$  and  $N_L$  were dominated by changes in temperature, rather than by other factors such as moisture or radiation. By contrast, between-community variation in  $P_L$  is controlled by substrate rather than temperature effects (Asner et al. 2016b). Along the Amazon-Andes gradient leaf N:P ratio declines with elevation (Malhi et al. 2017b) and this might indicate a switch from P to N limited photosynthesis consistent with soil properties (Nottingham et al. 2015, 2016), with Bahar et al. (2016) suggesting that knowledge of growth temperature is not required to estimate photosynthetic capacity if leaf and soil P data are available. Here, we used empirical relationships to infer the parameters of the photosynthetic light response curve form  $LMA$ ,  $N_{La}$  and  $P_{La}$  and thus determine how changes in traits regulate C-fixation. In an additional simulation exercise, the progressive increase of the functional strategies included in the model (from one PFT, to nine PFTs, to a continuum of plant strategies), increased

the predictive ability of the model. This outcome suggests that species turnover (Asner et al. 2014a; Neyret et al. 2016) and the associated shifts in plant functional traits is a stronger driver of spatial variation in forest productivity than direct environmental filtering effects (S5–Importance of elevation shifts in functional traits).

**Solar Radiation & Light Competition**

Along the Andean gradient, solar radiation declines at mid-high elevations, associated with a higher frequency of both cloud occurrence and cloud immersion (Halladay et al. 2012), and then rises again at the uppermost treeline plot. In our simulations, the actual photosynthetic rate follows variation in light availability, while at the uppermost plots this relationship could be additionally controlled by the higher photosynthetic light saturation level that characterises upland trees (Fig 4). Thus, solar radiation is the strongest direct climatic determinant of forest productivity, and therefore actual photosynthesis does not track potential photosynthesis (van der Weg et al. 2014, Malhi et al. 2017a). One of the key criticisms of classical MST is that it fails to account for asymmetric competition for light (Coomes & Allen 2009). The proposed modelling framework addresses this issue by explicitly simulating the hierarchical position of each individual within a stand, using the PPA assumption (Strigul et al. 2008). Our simulations show that inclusion of light competition is necessary for accurately predicting GPP and NPP (S5–Light Competition).

**Stand Structure**

Our simulations suggest that stand structure and in particular diameter distribution do not have a strong effect on forests productivity along our study plots. Although woody biomass declines with elevation, basal area does not (Malhi et al. 2017b). This constancy of basal area may diminish the effect of biomass variation in contrast with studies that identify biomass as the strongest predictor of forest productivity, for example during succession (Lohbeck et al. 2015). Thus in mature stands, like the ones studied here, variation in functional traits that control carbon assimilation and biomass allocation might be stronger predictors of forest productivity than standing biomass (Finegan et al. 2015). In our case this functional trait variation seems to be primarily controlled by species turnover.

**5. Conclusions**

Here we combine a uniquely rich dataset of plot-level productivity coupled with functional traits and a modelling framework to understand what drives the trend of productivity along a tropical forest elevation gradient. We have shown that an individual-based model that explicitly describes functional trait variation within and between plots, and accounts for light competition can

realistically capture variation in primary productivity along the investigated gradient. Our findings suggest that the decline in productivity with increasing elevation is explained by a combination of shifts in plant traits values and a decline in solar radiation. Remarkably, we do not need to account for direct temperature dependence of photosynthesis, beyond what may be an effect of temperature through the observed plant traits. The turnover in the plant community and ensuing shift in plant traits cancels much of the temperature dependency that is found in single plant in situ measurements. The work demonstrates the utility of tropical elevation transects in yielding important insights into long-term ecosystem sensitivity to temperature, but also suggests that variation in solar radiation introduces a moderate complicating caveat. Advanced new techniques such as airborne spectroscopy have demonstrated the potential to map key leaf traits at landscape and regional scale, both along elevation gradients and across edaphic contrasts in the lowlands (Asner et al. 2014a, 2016a). Our work shows that this spatial variation in traits can translate into potentially mapping spatial variation in productivity at landscape scale, with spatial variation in leaf traits capturing much of the spatial variation in environmental conditions. However, mapping traits alone is not sufficient, and there is still a need to account for light-limitation of photosynthesis. In combination with airborne mapping of canopy traits at large scale, this work opens the door to a mechanistic approach to mapping ecosystem productivity at landscape and regional scales.

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## TABLES

**Table 1:** Results of TFS performance under different setups. Bold values of the Pearson's correlation coefficient ( $\rho$ ) between field measurements and simulations indicate a statistical significant associations ( $p < 0.05$ ). In cases of significant correlations a SMA regression was fit and the slope  $\beta_{\text{SMA}}$  along with a 95% CI is reported. An adequate model performance is considered when  $\beta_{\text{SMA}}$  estimates include 1. RMSE ( $\text{Mg C ha}^{-1} \text{ y}^{-1}$ ) between observations and simulations are also reported with lower values indicating a better model performance. The slope of an ordinary least square regression of simulated productivity with elevation  $\beta_{\text{OLS}}$  ( $\pm$ standard error) is also reported here to summarise the sensitivity of GPP and NPP with elevation. For comparison the estimated slope from observations for GPP is  $-3.05 (\text{Mg C ha}^{-1} \text{ y}^{-1} \text{ km}^{-1})$  and for NPP is  $-1.53 (\text{Mg C ha}^{-1} \text{ y}^{-1} \text{ km}^{-1})$ .

Setup	$\rho$ simulations- observations	slope simulations- observations ( $\beta_{\text{SMA}}$ )	RMSE simulations- observations	slope simulations -elevation ( $\beta_{\text{OLS}}$ )
<b>GPP</b>				
<b>FcS:</b> Fully Constrained	<b>0.77</b>	1.03 (0.93-1.14)	3.25	-4.24 ( $\pm 0.90$ )
<b>CoS:</b> Local Climate	<b>0.79</b>	1.09 (1.00 – 1.18)	3.99	-1.40 ( $\pm 0.83$ )
<b>SoS:</b> Local Stand Structure	0.06		4.92	0.51 ( $\pm 0.41$ )
<b>ToS:</b> <i>Local Traits</i>	0.51		5.38	-3.26 ( $\pm 0.69$ )
<b>NPP</b>				
<b>FcS:</b> Fully Constrained	<b>0.90</b>	1.01 (0.93-1.10)	0.99	-1.40 ( $\pm 0.30$ )
<b>CoS:</b> Local Climate	<b>0.60</b>	1.07 (0.92-1.24)	1.99	-0.46 ( $\pm 0.27$ )
<b>SoS:</b> Local Stand Structure	-0.31		2.13	0.17 ( $\pm 0.13$ )
<b>ToS:</b> <i>Local Traits</i>	<b>0.62</b>	1.07 (0.93-1.24)	1.64	-1.08 ( $\pm 0.23$ )

**FIGURE CAPTIONS**

**Figure 1:** Environmental and biotic controls on primary productivity. Environmental factors such as radiation, temperature and precipitation can have direct effects (black arrows) on GPP and NPP and/or indirect effects (grey arrow) through the regulation of stand structure and functional composition (expressed here as the distribution of functional traits). Biotic controls related to the stand structure and its functional composition can also have direct effect on primary productivity (black arrows). However stand structure and functional composition are not only regulated by environmental factors as for example the biogeographic and disturbance history of the region could also play a significant role. In this study we explore the roles of a number of environmental and biotic controls (dashed and solid black arrows) and find that only two factors (traits and radiation; solid black lines) are required to explain the elevational trend in productivity. This study does not address how environmental factors influence biotic attributes (grey arrow).

**Figure 2** Observed and simulated GPP (upper panel) and NPP (lower panel) along the Andes-Amazon transect. Plot-specific values of climate, forest structure and traits distributions are employed. Black circles are observations ( $\pm 2$  standard error). Grey squares indicate simulation with no temperature dependence of photosynthesis but with functional traits shift along the gradient. Triangles indicate simulations with temperature dependence of photosynthesis and functional traits shift along the gradient. Open circles indicate simulations including temperature sensitivity but no functional traits shift along the gradient. Lines present local polynomial regressions (loess) of simulated GPP and NPP with elevation under the different model setups.

**Figure 3:** Simulated GPP (upper panel) and NPP (lower panel) under the different model setups. Grey points indicate GPP or NPP simulations following the fully constrained model setup (*FcS*). Green points present simulations using the local climate (*CoS*) and average regional structure and trait data. Blue points present simulations using the local stand structure (*SoS*) and average regional climate and trait data. Red points present simulations using the local traits distributions (*ToS*) and regional climate and stand structure data. Black points indicate estimates of GPP or NPP from field measurements  $\pm 2$  standard errors. Line presents local polynomial regressions (loess) of simulated GPP or NPP with elevation for each model setup.

**Figure 4:** Elevational variation of key stand-level parameters inferred from the fully constrained (*FcS*) model setup.  $S_0$  ( $\text{MJ m}^{-2} \text{y}^{-1}$ ) is the total annual incoming solar radiation at the top of the canopy,  $I$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) is the average annual light availability across all canopy layers,  $N_s$  (stems  $\text{ha}^{-1}$ ) the number of stems per area,  $LMA$  ( $\text{g m}^{-2}$ ) the basal-area weighted average leaf dry mass per area,  $N_{La}$  and  $P_{La}$  the average basal area weighted  $N$  and  $P$  concentrations,  $A_{\max}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) the average maximum photosynthetic rate,  $R_d$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) the average basal area weighted respiration rate,  $A_L$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) average annual basal area-weighted actual photosynthetic rate and  $K$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) average basal area weighted half saturation coefficient. Kendall correlations coefficients ( $\tau$ ) are displayed for all stand-level parameters where a statistically significant association with elevation was identified.

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## Control









